

JOURNAL OF THE BOMBAY NATURAL HISTORY SOCIETY

April 2003

Vol. 100

No. 1

BREEDING BEHAVIOUR OF THE GREATER ADJUTANT-STORK *LEPTOPTILOS DUBIUS* IN ASSAM, INDIA¹

(With one text-figure and two plates)

HILLALJYOTI SINGHA^{2,3}, ASAD R. RAHMANI^{2,4}, MALCOLM C. COULTER⁵ AND SALIM JAVED^{2,6}

Key words: Greater adjutant-stork, *Leptoptilos dubius*, breeding behaviour, incubation period, fledgling

We studied the breeding behaviour of the greater adjutant-stork *Leptoptilos dubius* (Gmelin), the rarest stork in the world at north Haibargaon — its traditional breeding colony in Nagaon (26° 21' N, 92° 45' E), Assam, India — during 1995-1997. Focal nests of early (September-October) and late (November-December) breeding storks in both the seasons, from nest building to fledging of the last young, were observed from dawn to dusk. Development of young from hatchling to fledgling and the associated parental behaviour were recorded in detail.

The incubation period was 35 days while the fledging period was 142 days. Parents left unguarded chicks at the age of 4 weeks; at 6 weeks the chicks could defend themselves, and at 9 weeks they attained juvenile stage. The overall breeding behaviour of the greater adjutant-stork was found to resemble its congeneric the Marabou stork *Leptoptilos crumeniferus*.

INTRODUCTION

Of the 20 storks found in the world, the greater adjutant-stork *Leptoptilos dubius* is perhaps the most endangered. Earlier widely

distributed in Nepal, Bangladesh, Myanmar, Thailand, Cambodia and South Vietnam (Baker 1929, Flemming *et al.* 1979, Ali and Ripley 1987, Hancock *et al.* 1992), this largest of Asian storks has drastically reduced in number, and is confined to the Brahmaputra Valley of Assam, India (Saikia and Bhattacharjee 1989, Rahmani *et al.* 1990) with a small breeding population of 100-150 birds in Cambodia (Mundkur *et al.* 1995).

The greater adjutant-stork is a colonial breeder. Very little information was available on its breeding biology (Kahl 1966, 1970, 1971; Baker 1935; Hume and Oates 1890; Saikia and Bhattacharjee 1990) prior to our study. We studied the breeding biology of the stork

¹Accepted February, 2001

²Department of Wildlife Science, Aligarh Muslim University, Aligarh 202 002, Uttar Pradesh, India.

³Present Address: Department of Zoology, Birjhora Mahavidyalaya, Post Office and District Bongaigaon, Pin 783 380, Assam, India.

Email: hqrgilq@sancharnet.in

⁴Present Address: Bombay Natural History Society, S.B. Singh Road, Mumbai 400 023, Maharashtra, India.

Email: bnhs@bom3.vsnl.net.in

⁵P.O. Box 48, Chocorua, NH. 03817, USA.

Email: coultermc@aol.com

⁶Email: sjaved@erwda.gov.ae

intensively in the north Haibargaon breeding colony at Nagaon for two successive breeding seasons from 1995-1997, right from its arrival at the breeding colony, including the development of the chick(s) to fledgling, up to its departure. The results were compared with those of other stork species.

STUDY AREA

The study site, north Haibargaon, is a traditional breeding site of the greater adjutant-stork at Nagaon (26° 21' N, 92° 45' E). It is a small, semi-urban town situated in middle Assam, on the southern bank of the River Brahmaputra. New buildings are being made very near the nesting trees, which are on private property, near human habitation. A few busy public roads intersect the nesting colony. Behind the houses, there are isolated patches of forest and mixed plantations. Shrubs are present under the tall bamboo *Bambusa* sp. and betelnut *Areca catechu* dominates the area. Kolong a small river, flows about 100 m from the colony.

The Brahmaputra Valley has four seasons: winter (December-February), pre-monsoon (March-May), monsoon (June-September) and the retreating monsoon (October-November). The average rainfall during monsoon is 286 cm.

METHODS

Chronology: The greater adjutant-storks aggregate at the colony in early September (Saikia and Bhattacharjee 1996a). Eggs are laid from September in Assam (Hancock *et al.* 1992). Storks were monitored daily from the first week of September, when they arrived at the site, till the end of May when all the nests were vacated. The adult storks on nests, and on nesting and non-nesting trees were monitored twice (morning and evening) daily.

Analysis: Monthly average of storks was calculated from the data collected. For analysis,

data of only those days when both morning and evening counts were taken was considered. Each nesting tree and nest(s) on it were assigned a code number to avoid counting error.

General Breeding Biology: Each year a tall watchtower (*machan*) was built to observe the colony. The height of the *machan* was equal to or just above the nests. Care was taken not to disturb the birds while building the *machan*. Once the birds started incubating, they did not desert the nest. They were observed till the focal nests were either vacated or abandoned. A nest was considered abandoned when the stork pair stopped visiting before laying the eggs, or if the eggs did not hatch and the pair left the nest, or if all nestlings died and the parents stopped attending the nest. A nest was considered vacated when the last nestling of the clutch fledged.

During the first breeding season, from November 1, 1995 to April 21, 1996, we observed five breeding pairs from a 20.5 m high *machan*. There were two trees with one nest each and one with three nests. From the last week of November to the first week of December 1995, three more nests were built on a tree where there was only one nest earlier. Out of the eight nests, five early ones (categorised as early breeders) were observed from the incubation stage, while the later nests (categorised as late breeders) were observed from the nest building stage. Since two nests were abandoned before the eggs hatched, and all the nestlings in one nest died, only five nests were observed till the fledging of juveniles. The average distance between the *machan* and the nests was 13 m.

During the second breeding season, from November 8, 1996 to May 12, 1997, we observed breeding pairs on three nests on three trees from a 23 m high *machan* from incubation till the juveniles fledged. The distances between the *machan* and nests were 12 m, 30 m and 60 m.

The breeding behaviour of the focal pairs was monitored continuously from dawn to dusk, 0500 to 1700 hrs, six days a week. However, the

duration of observation decreased to 11 hrs (0545 to 1645 hrs) a day during the shorter days of winter. It was assumed that the individuals seen in the late evening stayed through the night, as they were seen there again the next morning.

Individuals of the focal pairs were identified by their natural markings, facial and bill patterns and individual variations. Gender was determined by the copulation position. We found that the males were slightly larger than the females, which also helped to identify a male and a female of a pair (see also Kahl 1972a). We sketched facial patterns and noted the identification characters on 'face cards' (Coulter and Bryan Jr. 1988, Coulter 1989). The sketches were redrawn as the facial pattern of the stork changed.

We observed the breeding behaviour of other storks in the colony as far as possible. The morphological and behavioural changes from chick to fledgling stage were recorded. A chick was distinguished from a juvenile when blackish-brown feathers replaced its snowy white down feathers.

Incubation and Fledging Period: Incubation was estimated as the period from the initiation of incubation till the hatching of the first chick. The initiation of incubation was considered when, soon after nest building, the parents began behaving as if they were brooding eggs (Coulter 1989). It was difficult to know the exact date of hatching despite daily monitoring. The hatching at each nest was assumed on hearing the first call of the chick, or finding fresh broken egg shells below the tree, or observing the parent's posture and behaviour in the nest. In the focal nest, just after hatching, the parent stork would stand with its legs apart, point the bill towards the floor of the nest (to the new hatchling) and regurgitate or re-ingest food. Otherwise, when the chick was first seen, its probable age was subtracted to get the hatching date (Kahl 1966 and Pomeroy 1978a). In three cases where incubation period exceeded 55 days,

it was considered as probable re-laying of egg(s) and such nests were excluded from the analyses. The mean incubation period was calculated from five nests of both seasons, where egg laying and hatching was observed from the *machan*.

The fledging period was considered as the duration from the hatching to fledging of the juvenile, assuming that the same juvenile was the first chick. Before finally leaving the nest, juvenile(s) make exploratory flights and remain away from the nest for some time, and could be missed during a daily census. It was logistically difficult to see the first flight of all juveniles in the whole colony. Therefore, if a juvenile was not seen continuously for a week, it was regarded as fledged, and the fledging date recorded as the date it was last seen. We recorded the date of first flight in 12 nests from both the seasons, to calculate the fledging period.

RESULTS

Chronology: Data were collected over seven and nine months (November 1995 through May 1996 and September 1996 through May 1997) in the first and second breeding seasons, respectively. Storks were found to arrive at the breeding site from the first week of September. In both the seasons, the number of storks increased to a peak in the early part of the season and gradually declined to almost zero in May. In the first season (1995-96), the highest aggregation of storks was found in December, while in the second breeding season (1996-97), it was in October (Figs 1a & b). But the overall population trend in the study area was similar in both the breeding seasons. In all the months, in both breeding seasons, fewer number of storks were counted in the morning than in the evening.

General Breeding Biology

Pre-Chick Hatching Period: (a) External morphological changes: At the onset of the

BREEDING BEHAVIOUR OF GREATER ADJUTANT-STORK

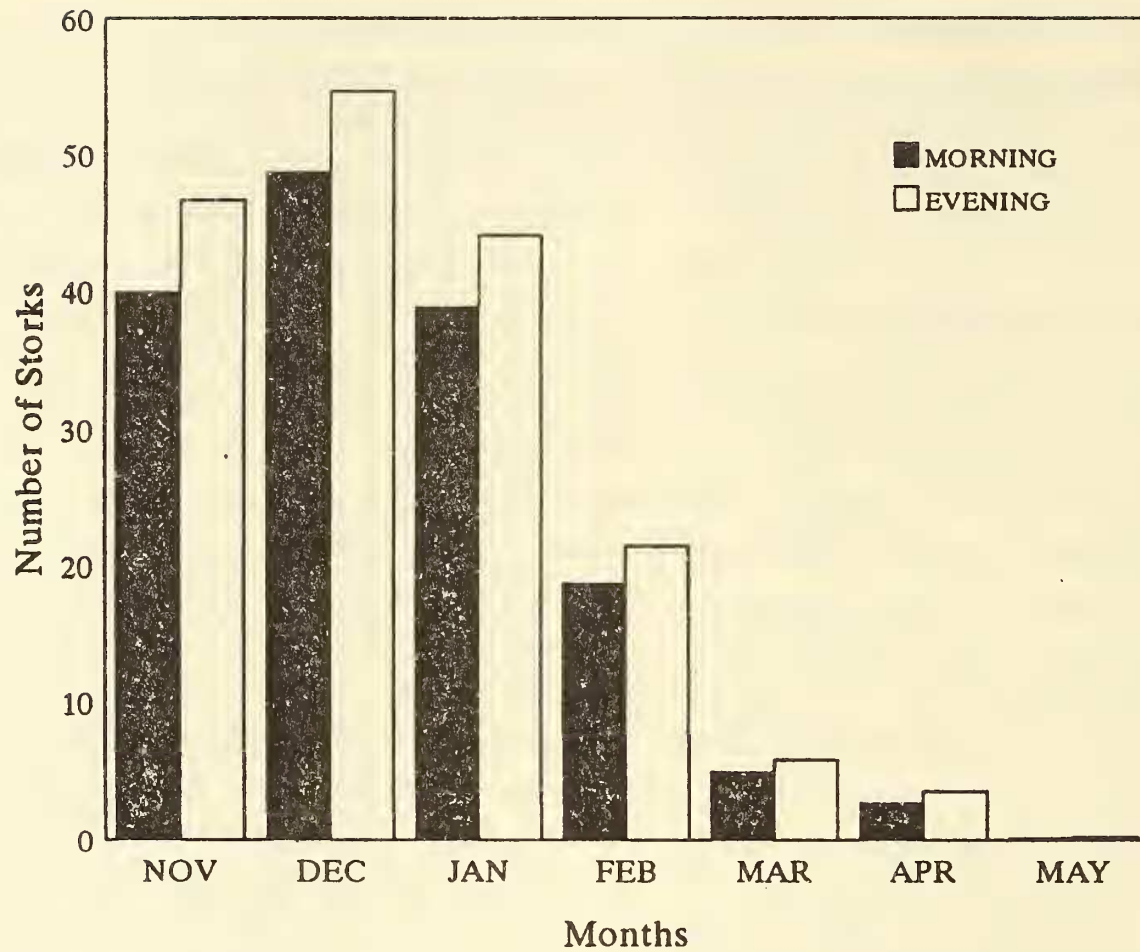


Fig. 1a: Population trend of greater adjutant-stork in North Haibargaon Nesting Colony (1995-96)

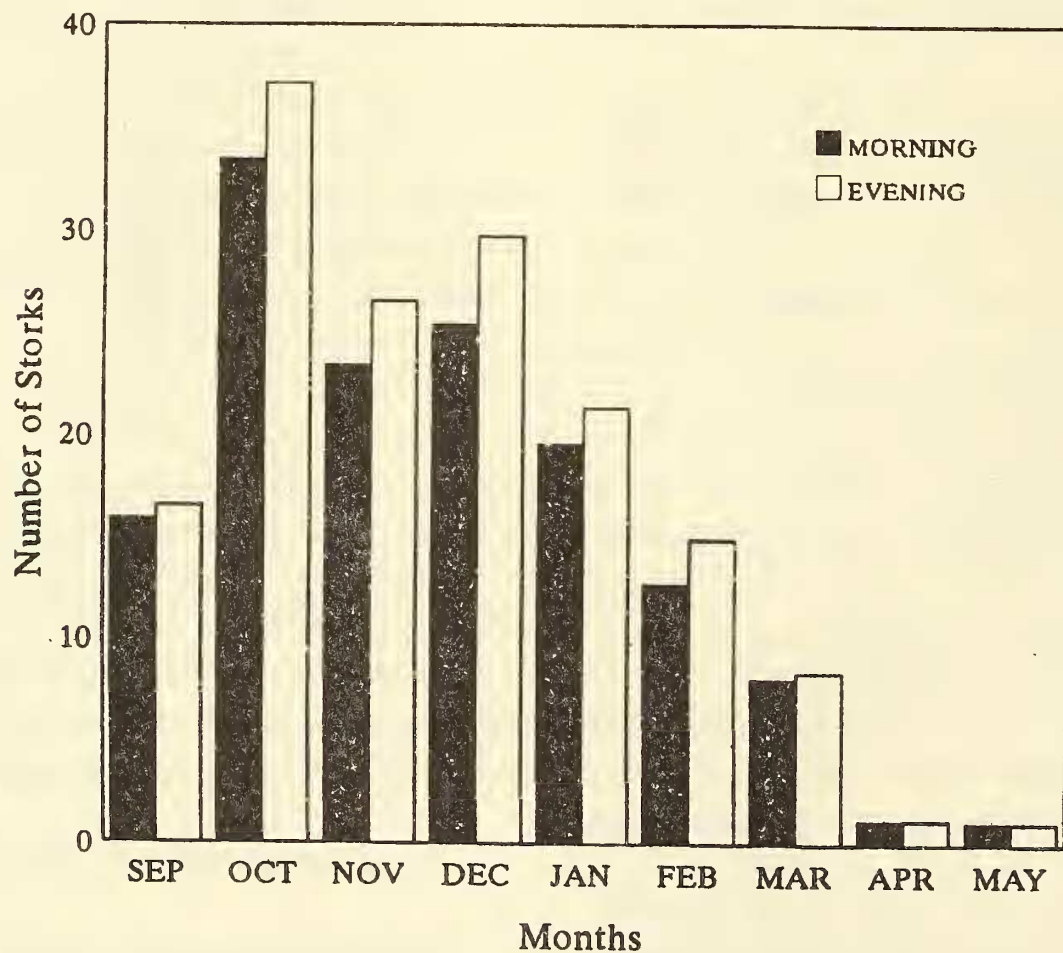


Fig. 1b: Population trend of greater adjutant-stork in North Haibargaon Nesting Colony (1996-97)

breeding season, the stork underwent conspicuous morphological changes to become a brilliantly coloured bird (Plate 1, Fig. 1). The pale whitish wing band of the greater secondary coverts of the non-breeding season became bright silvery white. The upper parts of the body including back, wing, tail and mantle turned to bluish-grey from slaty grey or blackish-grey. The under-tail coverts, which were white at their base and dark smoky grey at the tip, became fluffier. The head and nape became bright red. Black pigment appeared on the pale red part between the head and forehead. The skin of the face and forehead appeared rough and encrusted with dark spots. The base of the bill, just below the dark skin, turned pinkish. The neck turned bright yellow with a pinkish tinge. The dorsal air sac became bright red, encircled by a ruff of white feathers. The gular pouch appeared bright red.

We found that the female was brighter than the male. All breeding pairs wore the breeding plumage except one dull coloured male. There were some storks in the colony which, despite being brilliantly coloured, were smaller than an adult in size, and had a few erect 'hairs' on their head, and black 'hairs' hanging from the tip of the gular pouch. They were most probably younger storks or first time breeders.

As breeding progressed, the breeding pairs gradually regained their non-breeding colour. By mid January, the upper part turned ashy grey; head, neck and forehead became paler from bright red and black respectively. The silvery white wing band also faded. In April, they looked like non-breeding storks with blackish upper parts and a dirty wing band.

(b) Flocking: Breeding storks flocked in the beginning of the breeding season. There were some aggressive interactions, including chasing, fighting, squealing, bill clapping and frequent flying from branch to branch and tree to tree. Flocking occurred due to competition for pair formation and nesting sites. One stork would follow another, and within a short time many

storks would gather on a tree. At this time, a stork perched on a branch would stretch its wings, with a forward curve, bend its neck down and bring the open bill between its feet. At the same time, the tail would be cocked and the stork would make a long squeal 'qui-e-e-i', similar to the call of the black kite *Milvus migrans*, or a loud booming nasal sound 'we-i-nh'. The storks were also found to make loud and deep 'woom' sounds like the "lowing of a cow" (Hume and Oates 1890). The female was more vocal than the male, generally squealing and making nasal 'we-i-nh' noises, which gradually became faint later in the breeding season. This high-pitched vocalisation would be accompanied by occasional bill clapping with the bill pointed upward. A dull coloured stork and some subadult storks also visited the colony. However, they did not take part in the flocking.

Flocking would occur on one or two trees in the colony at the same time. Each stork made a small territory of its own and refused entry to other storks, whose approach resulted in ferocious fights. Sometimes flocking (crowding) occurred continuously for ten to fifteen days on a particular tree. These activities started in the morning, gradually declined at noon and again increased towards evening. While some storks formed pairs and selected nesting sites, the remaining moved to other trees for flocking.

These activities increased sharply to a peak in the beginning of the breeding season, and gradually ended in the latter part of the breeding season. While many storks settled down for nesting, some that were unable to find a partner still crowded around to disperse the pairs and invade the nests. We termed these as 'floating storks', most of which were probably first time breeders. Crowding was seen as late as the last week of January.

(c) Pair formation and courtship: During the process of crowding, a male stork would create a territory on a potential nest site, and chase other storks that came near him. He

announced his territory by frequent, loud bill clattering, pointing the bill upward, downward, or horizontally, and prodded the air with frontal arched body and half folded wings towards its breast. When he accepted a female stork, both perched closely to form a pair. A third stork, usually a female, was often found trying to break the pair bond. The female of the pair was more aggressive than the male in chasing away her rival. In two cases in the first breeding season 1995-96, we found that the third stork temporarily replaced the female of the pair, but was finally driven away. The male easily accepted the new partner.

In some cases, the new pair was found to perch close together continuously for two to three days, without foraging, before building the nest. We saw the pair take initiative in the courtship display, which varied only slightly among different pairs. A male would pluck a fresh twig from a nearby branch and put it near the feet of the female, or drop the twig after holding it for a few minutes. He would touch and gently grasp one of the female's tarsi with his bill. Sometimes the female also touched her own legs. She would withdraw her foot whenever a male grasped it. Once, a male pulled at one of her primaries. He gently clasped her bill, touched her breast in a preening gesture and gradually came closer to her. During this process they leapt to another branch or made a short flight to another tree with the second partner following behind.

When a female approached a male, she would lower her head to touch the male's breast with both her bill and head. He would cross his neck over hers and she adopted a submissive posture. Typical 'swaying twig-grasping' and 'up-down' displays (Kahl 1971, 1972a) were shown by both; however, the former was mostly shown by the male. The stork perched close to its partner bent its neck downward, pointing the bill down about 45°, and oscillated gently from side to side four to five times at half an oscillation per second. Sometimes, at the extreme ends of

an oscillation, it would pull or touch a twig and give a mild jerk. Both the partners perched side by side, sometimes preened themselves and showed an up-down display simultaneously or one by one. The bill was then sharply brought down almost touching the breast, or abdomen or feet with a sudden loud nasal 'we-i-nh' immediately followed by throwing it upwards pointing vertically towards the sky. Thus, they clattered their bills, stopping only after the bill was again brought down below the horizontal position. The clattering ceased before the bill was brought to a horizontal position in brief bill-clattering sequences.

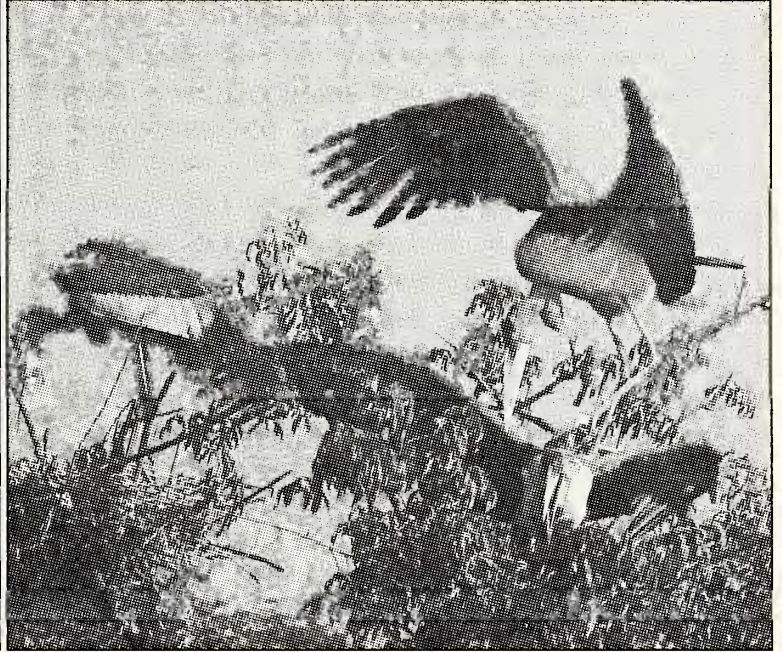
(d) Mating and nesting: Usually, the courtship display was followed by mating which occurred on the nest-branch or in the nest. Only twice was mating seen outside the nesting tree. Just before mating, in most cases, both the partners stood side by side in close contact. The male lifted one of his legs onto the back of the female and mounted (Plate 1, Fig. 2). He either mounted from the side, or from the front or rear, standing on her shoulder for a few seconds and then positioning himself for copulation. As soon as the male mounted, the female bent her 'knees' in a submissive posture, both the wings spread for balancing. During copulation, the male flapped his wings vigorously and sometimes snapped his bill frequently. The bill clattering usually started as soon as he copulated, at times simultaneously with mounting. On a few occasions, the sound of the bill clapping was not heard. During copulation, the female lowered her open bill 45°, swayed it from side to side and made a moaning sound. The male usually clasped the female's bill and clattered against her bill. After copulation, he stood on her shoulder for some time. Mating was sometimes followed by preening.

The whole process of mating ranged from 11 to 68 seconds (average 25.56 ± 10.38 sec, $n = 52$). Mating occurred 1-6 times a day, between 0545 and 1635 hrs. Out of 141 matings observed,

1



2



3



4



Figs 1-4: Greater adjutant-stork *Leptoptilos dubius*: 1. Adults in breeding plumage, 2. Adult male mounting on a female, 3. Parent tending one week old chick, 4. Adult feeding two week old chicks

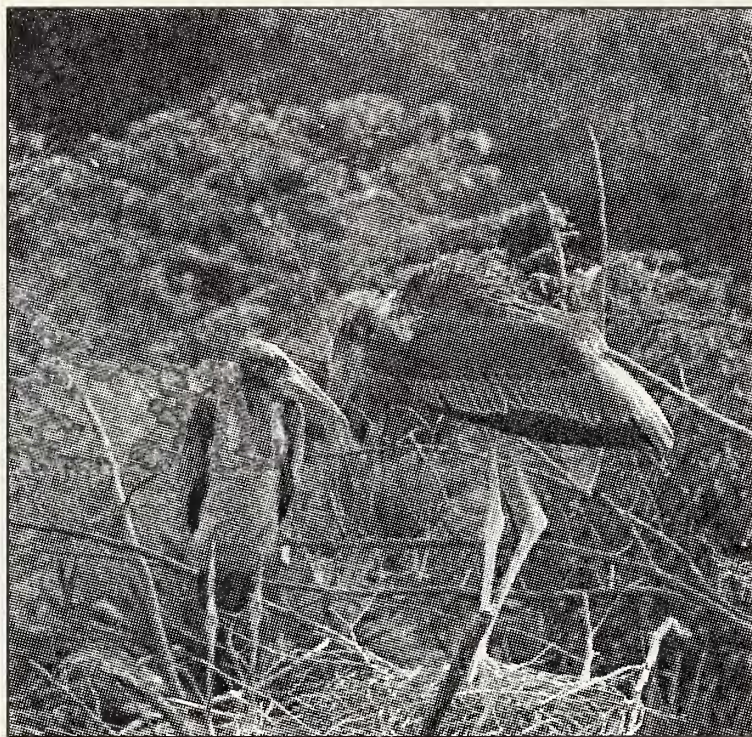
5



6



7



Figs 5-7: Greater adjutant-stork *Leptoptilos dubius*: 5. Parent with four week old chick, 6. Parent tending six week old chick, 7. Nine week old juvenile

81 (57.45%) occurred in the forenoon, and 59 (41.84%) in the afternoon. One was seen at mid-day. Mating was more frequent during nest building and early incubation. However, late mating was seen in four pairs whose first chick was 26, 32, 43 and 45 days old, respectively.

Simultaneously with mating, nest construction began. The male would place a green leafy twig on a flat horizontal branch, with or without an erect limb. The female stepped on it to hold it down, and soon the base was formed by piling one twig upon another. During the initial stages of nest construction, the female stood guard at the nest, while the male brought most of the nest material from the same or other trees in the colony. The stork did not go beyond 200 m to bring nest materials. Usually, mating occurred after frequent nest material trips by the male. During nest building, the female became more vocal, making a loud booming sound, accompanied by bill snapping. The male responded by clattering his bill when he reached the nest. Both sexes arranged the nest material. They would remove leaves from the nest and drop them as if cleaning the nest. In the early stages of nest building, the male generally roosted with his partner in the nest or near the nest. The nest construction took 2 to 4 days. Soon after that, the female spent more time on the nest, until she laid the eggs. Then the male took care of the nest, relieving the female for longer periods.

During nest construction, the male and female never left the nest together, but on two occasions the storks were absent from the nest (11 and 36 minutes) to collect nest material.

Incubation: The eggs were laid asynchronously and the incubation started as soon as the first egg was laid. The newly laid eggs were chalky white, with a green and blue tinge, which became soiled as the incubation proceeded. Both male and female incubated. During incubation (34.6 ± 2.70 s.d. days, $n = 5$), the incubating stork preens, flaps and stretches its wings, it rearranges and repairs the nest,

rotates the egg(s) and protects the nest from other storks and birds. When the bird stands up after a long bout of incubation, it shakes its body, stretches its neck forward with an open bill slightly downwards and changes its orientation for the next phase of incubation. It rotates the eggs to different positions by grasping them with the bill or shovelling them towards its feet with the tip of the beak. It then tilts the nest slightly with its feet, and the eggs roll back to the depression in the middle of the nest.

Post-hatching period: a) Growth of chicks and associated behaviour of parents: The growth rate of the chick varied in different nests. A general pattern of growth and behaviour of the chick is described below.

The chicks hatch at intervals of one or two days. The newly born chick is about 10 cm tall, and has a pale yellow, slightly curved down beak and a large blackish head, and neck with yellow patches. Dorsally, the body has bluish-black down feathers, and pink underparts. The eyes are large and black; the swollen eyelids are blackish, while the forehead is sky blue. The chick grows fast and becomes double its size within a week, with white down feathers almost covering the back. During the first week of their life, the chicks spend most of the time sleeping.

When a chick hatched, the parents stood with legs apart and tended the baby frequently. The behaviour and posture of the parent indicated egg hatching (Plate 1, Fig. 3). The chick made feeble sounds, which became louder with time, into chittering. Both parents fed the young. The parents regurgitated food on the floor of the nest and the chicks picked it up. Soon after hatching, the parents started regurgitating black, granular half-digested food matter, so that the hatchlings could feed easily. The feeding frequency by regurgitation was higher in the early stages. Initially, the chicks could not consume all the food brought to them; the excess was re-ingested by the parent, and regurgitated later. While re-ingesting, the parent pressed large portions of

food between its mandibles to soften and crush it, so that the chicks could devour it easily. We found that although the parents would not feed the young bill to bill, it would help by holding the food such that it could be easily swallowed. The chick would jerk the food, toss its head forward and backward quickly and swallow the food. The chicks were found to be voracious feeders right from hatching. Even a day old chick tried to swallow a frog, much larger than its head! In one case, a three-day old chick gulped a fish that was larger than its body length; for some time the tail of the fish protruded outside its bill.

At two weeks (Plate 1, Fig. 4), the white down feathers completely covered the body of the chick, however, the underparts were still pinkish. The yellow patches on the head almost disappeared. The eyelids became whitish. The forehead or shield turned white with black spots. Dark black pigment spreads over the cheek. The ventral side of the throat was covered with dark black pigment in longitudinal bands. Dorsally, the neck was greyish and the shoulders black. Erect grey and white 'hairs' grow on the head and neck. The ill-developed sky-blue pouch could be distinguished. Beneath the wings and near the flanks, black feathers developed. The legs and toes became pinkish in colour.

Generally the parents relieved each other after more than 24 hrs. The reliever brought food for the chick(s) once a day. For about two weeks, most of the parents' time was spent in brooding the chicks and after that, in standing guard. However, in the morning and evening, and during rain they brooded and sometimes shaded the young. The parents also provided shade to the chick(s) by stretching their wings and standing against the sun.

The 3-week old chick is covered all over with snow white foamy down feathers, except ventrally. The bill is pale yellow with black marks at the base. Black 'hairs' hang from the tip of the pouch and on the shoulder. Pupils black, iris brown. Legs pinkish-white.

The 4-week old chick is about 30 cm in height. The shield is still white with black spots. The grey and black crest of thick 'hairs' grows longer. Down the throat, and ventrally, longitudinal black patches are prominent. Black primaries and secondaries start to grow. Black tail feathers also appear.

At 4 weeks, a chick can stand on its feet and flap its wings 4-5 times at a stretch (Plate 2, Fig. 5). The wing span is approximately 60 cm. The chick walks in the nest. The parents also gradually start leaving the nest, initially for short durations only. When the parents return with food, the young ones perform typical begging displays. They drop down to their tarsi opposite each other (if more than one young), wings half folded, slightly lifted upward, body bent forward, tail cocked and toss their heads up and down rhythmically with open bill and nasal 'honk-honk' sound.

In the 5-week old chick, the primary feathers of the wings start developing. Initially they have a black tip and bluish rachis. The primaries at the tip of the wings are now larger, about one and half inches. The tail feathers become more prominent. The pinkish white legs turn whitish. The longitudinal black patches of the throat become concentrated only on the pouch. The ear opening is surrounded by a white mark. At this stage, a chick tries to leap in the air, frequently flapping its wings. It defecates over the edge of the nest and swallows food very fast.

A 6-week old chick is fully covered by thick down, which has changed from snowy white to dirty white (Plate 2, Fig. 6). The black spots on the shield are almost gone. The sky blue throat pouch, with pink tinge at the base, and sparse black pigments, becomes elongated. The black 'hairs' hanging from the pouch become longer. Black feathers on the shoulder around either side of the base of the neck turn brownish and grow to meet at the breast, forming a necklace-like band. The wings develop four layers of feathers: the lowermost black primaries are concealed by

a broad brownish band of greater secondary coverts, and two more black layers above the second layer. Twelve broom-shaped fan feathers with blue rachises grow at the tail, black horse-shoe shaped flat feathers at the tip, followed by thin grey 'hairs' hanging from it.

At this stage, the parents even stay away from the nest at night as the chick is able to defend itself. It would even threaten a crow or a kite hovering overhead by poking its head towards the intruder, with a harsh 'khll-o-ck' sound. When other storks came near the nest, it sat down on its tarsi, faced the intruder with half folded wings, and tossed its head up and down, emitting a nasal 'khll-i-ck khll-i-ck' sound rhythmically with movement of the head till the intruder flew off. At this stage, the chicks also clean the nest like adults.

By 7 weeks, another row of black feathers developed just above the fourth layer on the wings. Two longitudinal rows of black feathers were growing on either side of the midline of the mantle. When the wings were folded, three-fourths of the upper part was covered by black feathers. At this stage, the parents came to the nest only to feed the chick(s). The chick flapped its wings more frequently, 10 to 12 times at a stretch.

At 8 weeks, six rows of black feathers appeared on the wing. The tail fan became elongated and expanded. While flapping the wings, the chick tried to lift itself up in the air.

Throughout the fledgling period, the parents occasionally nursed the chick. Up to 3 weeks, they would gently touch the head and body of the chick, but later they also preened the chick.

(b) Growth of Juvenile and associated parental behaviour: At nine weeks, the chick attained juvenile stage (Plate 2, Fig. 7). It almost equalled its mother's height. The upper parts became completely black. The broad brown layer of the secondary coverts became more distinct. The shield was white with very few black spots.

The bill was pale yellow. The ear opening surrounded by white mark became more prominent. The pupil was black and the iris brown. Near the eyes and on the cheek, black spots were sporadically present. The thick crest of black and grey 'hairs' on the crown and neck were longer, and so were the 'hairs' at the tip of the whitish pouch. The legs became creamish-white.

The juvenile's food was supplemented with pieces of meat and intestinal parts of mammals in addition to fish, amphibians, reptiles and birds. Gradually, it can leap straight upward 1-2 m in the air with vigorous flapping of wings. This leaping is more frequent when the wind blows. At about four months, the juvenile flies from one branch to another and then to the other trees in the colony. It can chase other intruders from its nest. Sometimes it flies outside the colony and comes back to the nest to be fed by the parents. It can also be seen on other nests in search of food and nest material. The parents feed the juvenile till it fledges. The fledging period was about 142 days (141.94 ± 22.45 days, $n=35$). The first flight of the juvenile was seen at 126.25 ± 9.35 s.d. days ($n=12$). The fledging period ranged from 96 to 173 days in the first breeding season, and 110 to 197 days in the second breeding season in different nests. The juvenile fledged asynchronously; not necessarily the older sibling leaving earlier.

Other Breeding Behaviour: Greeting display: Greeting display between a pair commences soon after pair formation. It gradually declines by the time the chicks reach juvenile stage, because the parents hardly come to the nest at the same time. Among the greeting display, the up-down display and bill clattering were common. Usually when a partner arrives at the nest, the other partner greets it by upward bill clattering. Then both demonstrate an up-down display. Each stork could recognise its partner from a long distance; even about 100 m. When nest material was brought by the male, he

generally uttered a low pitched 'kis-kis' sound with one second pause after each 'kis'. The female brought nest material with nasal 'we-i-nh we-i-nh' sound. In the early part of the breeding season, a female greets the male with her long typical squeal, swaying the bill from side to side. When a female arrives on the nest, the male sways his bill from side to side, bowing down his head with a typical 'kis-kis' sound. When a male reaches the nest, the female sways her down-pointed bill from side to side, and places the nest sticks in accordance with the movement of the bill. Downward short duration bill clattering was also observed to greet each other. Sometimes there was no greeting display.

Aggression: Agonistic behaviour was seen more in the beginning of the breeding season. Aggressiveness also varied according to the individual and the situation. Generally, the female appeared to be more aggressive. Storks were found to chase other storks, which approached their nest, sometimes leaving behind an unprotected nest with egg(s) or chick(s). A stork could chase another stork up to 100 m, flying at it with a stretched neck and loudly snapping bill. Loud bill clattering was not only a greeting display, but also a threat to the other storks. Sometimes a breeding stork was found to tolerate the presence of other storks and even crows very near its nest.

In the early part of the breeding season, during nest building, and even during incubation, some storks try to invade other nests for occupation or to replace a partner from an established pair. A case of nest invasion occurred in the first breeding season when one pair occupied the nest of another pair. Once a stork was also found to snatch food from another stork's nest. While fighting they poked their bills at each other's head in quick succession. Post flying juveniles were also found to be aggressive towards other adult storks that tried to enter their nest.

Nest arrangement: Storks repaired and cleaned their nest throughout the breeding period, but this activity progressively decreased as the young grew up. The storks cleaned the nest by removing egg shells and decomposed old leaves from the interior of the nest. They frequently picked up leaves by inserting one third of the bill into the huge nest and threw rotten leaves outside the nest. They grasped sticks and placed them, pulling and pushing them all along the nest rim and also at the bottom. Standing on one leg at the centre of the nest, the bird slowly placed the sticks along the periphery, so that a shallow depression developed at the centre of the nest. Sometimes this would continue for more than half an hour.

Nest material stealing: On finding an unguarded or vacated nest, storks stole nest materials. Even a five-month old juvenile was seen stealing sticks from empty nests. Sometimes they would rob nest material in the presence of its owner.

Father-offspring mating: What appeared to be father-offspring mating was seen in one nest in both the breeding seasons. The adult male suddenly placed one leg on the back of one of his young and mounted it. He stood on the back for 12 to 20 seconds and came down. Sometimes he appeared to copulate with the young, with or without mild bill clattering. The young uttered harsh chittering. In the first breeding season, this was observed ten times when the young were 9 to 11 weeks old. In the second breeding season, it was observed twice when the young ones were 5 and 9 weeks old.

DISCUSSION

Chronology: The greater adjutant-storks arrive at the North Haibargaon breeding colony just after the monsoon, when the dry season begins. In both the breeding seasons, the time of arrival was identical suggesting that the storks follow a definite time frame for breeding. The

nesting period synchronises with the reducing water level in the lakes and ponds (Saikia and Bhattacharjee 1996a, Bhattacharjee and Saikia 1996). All other breeding storks in India, painted stork *Mycteria leucocephala*, white-necked stork *Ciconia episcopus*, black-necked stork *Ephippiorhynchus asiaticus*, Asian openbill stork *Anastomus oscitans* and lesser adjutant-stork *Leptoptilos javanicus* breed just after monsoon (Ali 1996). In Assam, from September onwards water level gradually recedes with the decreasing rainfall. This period also coincides with the increase in availability of prey species, as many species of fish and frog breed during monsoon in the inundated low-lying areas. When water level drops, they concentrate in drying pools and puddles and become easy prey for the stork.

Most bird species breed around the time when food supplies are readily available (Thompson 1950). In the congeneric Marabou stork *Leptoptilos crumeniferus*, breeding usually begins in dry season and ends in rain (Brown *et al.* 1982). Pomeroy (1978b) also states the possibility of an intrinsic (circannual) rhythm for nesting period in the Marabou stork. The American wood stork *Mycteria americana* initiates nesting when water level goes down (Kahl 1964). Seasonal rains strongly influences the beginning of nesting in the Maguari stork *Ciconia maguari* (Thomas 1985). It seems that food supply and seasonal change with shorter days correspond to initiate breeding of the greater adjutant-stork in North Haibargaon breeding colony.

The population trend throughout the breeding season in both years of our study suggests that as the breeding season progresses, the greater adjutant-storks start leaving the colony. The storks that did not build nests leave the colony; the parent storks also spend less time in the colony when the young grow up. In the second breeding season it was seen that the number of storks reached a peak in October (Fig. 1b) when almost all breeding storks had

arrived in the colony. In both the seasons there was a small population peak in December (Figs 1a & b). This could be due to the late breeders who returned to the colony. A similar second small peak was seen in a painted stork colony by Urfi (1993), which he speculated could be due to a second breeding attempt or prolonged breeding effort. In Maguari stork also, late-arriving individuals begin to build nests well after the beginning of the breeding season (Thomas 1986).

The reason for smaller numbers of storks in the morning count is probably because some storks leave very early for foraging, much before sunrise. In the evening, all the storks returned to roost, so more birds were seen.

General Breeding Biology

External morphological changes: The external morphological changes in the greater adjutant-stork during the breeding season were similar to the observation of Saikia and Bhattacharjee (1996a) and, Bhattacharjee and Saikia (1996). Similar changes occur in the Marabou stork also (Brown *et al.* 1982). Pomeroy (1977b) found that males of the Marabou stork were considerably larger than females, which we found in greater adjutant-stork also. Kahl (1972a) has reported this earlier. In painted stork (Desai *et al.* 1977) and American wood stork *Mycteria americana* (Kahl 1962), males are larger than females. The brighter coloured female approaches the male to initiate courtship. Competition for pair formation was between females for the male who had selected a potential nest site.

Flocking and aggressive behaviour: Lack (1968) also observed that in some colonial species, the sub-adults also come to the breeding sites, form pairs, occupy nesting sites and build nests, but do not proceed further. We found some sub-adults and some probable fresh adults arriving in the colony. Bhattacharjee and Saikia (1996) also observed that both sub-adults and

non-breeding greater adjutant-stork also came to the nesting colony, but Pomeroy (1977a) observed that it does not necessarily follow that all storks in breeding plumage are sexually mature. The minimum age at first breeding is 4 years in Marabou stork (Pomeroy 1977b), and 3 years in male and 4 years in female in Maguari stork (Thomas 1984). According to Bhattacharjee and Saikia (1996), the greater and lesser adjutant-stork become sexually mature at 3-4 years. Lack (1968) has explained the arrival of the sub-adults at the breeding colony as the preparatory year to learn the best feeding areas around their nest without the strain of finding food for a brood.

Bhattacharjee and Saikia (1996) reported rigorous vocalization and 14 to 16 storks flying together from tree to tree in the early part of the breeding (September), what we have called 'flocking'. Coulter (1989) has termed the aggressive interactions in American wood stork as 'mobbings' and Kahl (1972b) has referred to them as "bachelor parties". Although aggression was always associated with crowding, fight was not between two storks; instead a flock of five to fifteen greater adjutant-storks took part together in this activity. The aggressive interactions of 'mobbings' in American wood storks were moderately frequent in the early part of the breeding season, and rose to a peak in the following weeks correlating with an increase in nest building, and declined gradually (Coulter 1989). We observed the same in the greater adjutant-stork.

We observed that in greater adjutant-storks aggressiveness varied individually, and female storks seemed to be more aggressive. While Thomas (1986) noted that attacking Maguari storks were mostly males. Though female American wood storks are generally less able to defend themselves (Coulter 1989), we found that greater adjutant-stork females even invaded other nests. As Coulter (1989) recorded nest invasion in American wood stork, we found a similar case

in greater adjutant-storks too. The replacement of one incubating female American wood stork by another pair and throwing out the former's egg was observed in greater adjutant-storks also, but in the case of greater adjutant-storks the aggressor was a female. Moreover, while guarding a nest with eggs or chicks, a female sometimes chased away others near the nest, leaving the nest unguarded. Such behaviour was not seen in American wood storks by Coulter (1989) who found that unguarded chicks were thrown out by neighbouring storks. Similarly, in greater adjutant-storks, while pulling nest sticks from an unattended nest, the "robber" stork attacked the defending chicks, of which, two 3-week old chicks fell out.

The 'aerial clattering threat' described by Kahl (1972a) was also observed in the greater adjutant-stork. According to him, lesser adjutant remains silent while chasing another stork in the air, but Marabou clatters loudly as the opponent is approached closely. Similar behaviour was observed in the greater adjutant-stork.

The other hostile display described by Kahl (1972a) such as snap display, pre-flight snap, erect-gape and anxiety stretch were noticed in the greater adjutant-stork. However, forward poking, which is similar to 'forward display' behaviour in herons (Meyerriecks 1960; Tomlinson 1976), was not mentioned by him. In this behaviour, two greater adjutant-storks stand erect on their nest or branch face to face and poke at each other, sometimes with a bill snapping sound, frequently but hardly any physical contact. Sometimes a greater adjutant-stork was also seen shooting its bill sharply in horizontal direction in the air when the opponent was at a distance.

Pair-formation, courtship and greeting display, mating and nesting: In many aspects of morphology and behaviour, the greater adjutant resembles its African cousin, the Marabou stork (Kahl 1974), but it is closer to the lesser adjutant (Kahl 1970). We saw the same

'swaying twig-grasping' as described by Kahl (1972a) for the greater adjutant and Marabou stork. For the first time we observed side to side swaying of the bill by a male greater adjutant to greet a female partner at her arrival to the nest with "kis-kis" sound. This behaviour can be compared with the 'advertising sway' of the Asian openbill stork described by Kahl (1971). The differences are; (a) greater adjutant-stork did not lift its feet with each oscillation; and (b) greater adjutant-stork makes a typical sound. The female greater adjutant also greeted the male in the nest by swaying downward pointing bill and arranging nest sticks. Similar 'twig passing display' is seen in the great white egret *Egretta alba* (Tomlinson 1976), where the female greets the male on his arrival to the nest by 'stretch display'.

The most common greeting display in the greater adjutant-stork is the up-down display that Kahl (1971) has seen in all except the Saddlebill stork. He has mentioned that all the three species of *Leptoptilos* give frequent up-downs whenever a member of a pair returns to the nest. But we found that the greater adjutant did not give an 'up-down' display every time its partner arrived at the nest.

Kahl (1970, 1971, 1972a and 1974) emphasised on the difference between Marabou storks and both the adjutants in up-down display. In the former, the bill is first thrown upwards and vocalizations are made, then the bill is pointed downwards and clattered. In the latter the bill is directed upward during both vocalizations and clattering. We also observed the upward bill clattering, but would like to stress that the clattering did not always cease before the bill reached horizontal position; sometimes clattering stopped only after the bill pointed downwards. On some occasions we observed one member of the pair greeting the other by short downward bill clatterings. Vocalization of the lesser adjutant is hoarser and more rasping than the greater adjutant (Kahl 1970).

There is no literature regarding the mating behaviour of greater adjutant-storks. However, it was found that the loud copulation clattering of greater adjutant-storks resembles that of other storks, except Asian openbill storks where the male does not clatter his mandibles loudly (Kahl 1970). The balancing posture of the female during copulation is similar to that of other storks except the white stork where the female does not spread her wings wide (Kahl 1971) and the Jabiru stork where the female usually opens her wings fully at first and then closes them partially after the male is in position (Kahl 1973). The occasional post copulation preening in greater adjutant-storks is also found in other storks, e.g. painted storks (Desai *et al.* 1977) and Maguari stork (Thomas 1986). The copulation duration of greater adjutant-storks (25.56 ± 10.38 sec) is found to be the longest among storks: 10 sec in painted stork (Desai *et al.* 1977), 8.77 ± 1.15 sec in Maguari stork (Thomas 1986), 24 sec in black-necked stork and 15 sec in Jabiru stork (Kahl 1973). Late mating, as we found in greater adjutant-storks, is also reported in painted storks where copulation occurred even after the fledging of the young (Desai *et al.* 1977). However, attempted father-offspring mating behaviour is not reported in other storks. It was, however, not known if the young was a male or female.

Development – egg to fledgling: Our description of freshly laid eggs of greater adjutant-storks is similar to what was described by Hume and Oates (1890). The asynchronous laying of eggs is also reported by Saikia and Bhattacharjee (1996a). Lack (1968) states that in Ciconiiformes, the successive eggs in a clutch are laid two or more days apart, incubation starts with the first egg, and the young hatch one or more days apart.

The development of the chick to fledgling stage and associated parental behaviour are more or less similar with other storks. The stork nestlings spend most of their time between meals sleeping and thereby reduce energy demands

(Kahl 1962). The rapid early growth pattern exhibited by altricial birds, aids to survival in several ways. A four-week old greater adjutant tried to leap in the air with flapping wings. The Marabou chick can stand and flap wings in 17 days (Brown *et al.* 1982) and Maguari chick can stand in 22 days (Thomas 1984). The postures, movements, and vocalizations in the begging display and nesting defence display of both Adjutant species were quite similar to the Marabou stork (Kahl 1972a). However, in solitary breeding storks, vocalization of the chicks are not as loud as those in colonial species (Kahl 1973).

Incubation and Fledging Period: Pomeroy (1978a) estimated the age of the young "fairly accurately" from their appearance to get the date of hatching, but our observations on different nests indicated that it would definitely vary. We found that individual chick growth was quite varied, i.e., a particular stage could not be always assigned to a particular age. Some chicks grew faster than the others.

The incubation period of the greater adjutant is around 35 days as observed in the five focal nests. Except for the five nests, prolonged incubation period exceeding 35 days was noticed in some other nests. In one case, even when the first chick had grown to 30 days, an egg was still being incubated. Finally, it was dropped from the nest. Prolonged incubation has been reported in a number of bird species (Skutch 1962, Afik and Ward 1989). Drent (1975) suggested that prolonged incubation was a functional response caused by the inherent variability in incubation period. Marks (1983) thinks that prolonged incubation behaviour is related to the time interval in which the entire clutch would normally hatch. This does not seem to be the case in greater adjutants whose clutch size is small and eggs hatch simultaneously. Prolonged incubation is also reported in painted stork (Desai *et al.* 1977). Pomeroy (1978a) reports that one pair of Marabous' incubated for

150 days, and eventually one young fledged from that nest. He regarded it as re-laying of eggs in the same nest, which he found was 8% in Marabou stork. We also found 7.5% cases of probable re-laying in greater adjutant-storks. In three nests, we also noted a prolonged incubation period of 93, 97 and 107 days, which we suspect was re-laying.

According to Lack (1968), the incubation period in Ciconiidae varies between 30-33 days. Incubation period in greater adjutants reported earlier is 30 days (Saikia and Bhattacharjee 1996b). It seems that our estimate of incubation period of 35 days is longer than in other storks: 32 days in American wood stork (Heinzman and Heinzman 1965), 32 days in white stork (Schuz 1972), 29-32 days in Maguari stork (Thomas 1984, 1986), 32 days in painted stork (Desai *et al.* 1977), 30-31 days in white-necked stork (Scott 1975), 28-30 days in Abdim's stork *Ciconia abdimii* (Farnell and Shannon 1987) and 29-31 days in Marabou stork (Brown *et al.* 1982, Kahl 1966, Pomeroy 1978a).

The fledging period of greater adjutant-storks was about 142 days. The fledging period in Marabou stork was 132-135 days (Kahl 1966, Pomeroy 1978a). There was a gap of 67-74 days between first and last fledging in the greater adjutant-stork colony. We also found that young which hatched earlier did not necessarily fledge earlier. Even siblings of the same nest fledged asynchronously. However, we could not find out the exact fledging period according to the first flight of the nestling, as it was impossible to monitor all the nests of the colony continuously. However, we were able to calculate the duration of hatching to first flight in a few nests (*c.* 120 days, *n*=12) which was closer to the fledging period in Marabou stork.

Comparing its biology with other storks, it appears that the greater adjutant-stork resembles, in most of its behaviour and biology, its congeneric the Marabou stork. The long breeding season of this colonial bird is an

important phase in its life cycle, during which the crucial need seems to be food.

ACKNOWLEDGEMENTS

We are grateful to the US Fish & Wildlife Service, especially to Mr. David Ferguson, SFC coordinator, for funding the project and the

Ministry of Environment & Forests, Government of India for sponsoring it. We thank our field assistant Mr. Dwipendra Narayan Dev for assisting us throughout the fieldwork. We thank Mr. J.C. Daniel, Honorary Secretary, and Dr. Ranjit Manakadan, Senior Scientist, Bombay Natural History Society for their suggestions.

REFERENCES

- AFIK, D. & D. WARD (1989): Incubation of dead eggs. *Auk* 106: 726-728.
- ALI, S. (1996): The Book of Indian Birds. 12th edn, Bombay Natural History Society, Mumbai. 354 pp.
- ALI, S. & S. D. RIPLEY (1987): Compact Handbook of the Birds of India and Pakistan together with those of Bangladesh, Nepal, Bhutan and Sri Lanka. 2nd edn, Oxford University Press, Mumbai. Pp. 737.
- BAKER, E.C.S. (1929): The Fauna of British India, Vol. 6. Taylor and Francis, London. U.K. Pp. 499.
- BAKER, E.C.S. (1935): The identification of Birds of the Indian Empire, Vol. 4. Taylor and Francis, London. Pp. 546.
- BHATTACHARJEE, P.C. & P.K. SAIKIA (1996): Conservation of Greater Adjutant-Stork in Assam. Final Technical Report. WWF - I Project 4630. Pp 89.
- BROWN, L.H., E.K. URBAN & K. NEWMAN (1982): Birds of Africa, Vol. 1. Academic Press, London. Pp. 521.
- COULTER, M.C. (1989): Wood Storks of the Birdsville Colony and Swamps of the Savannah River Plant. 1989 Annual Report. Savannah River Ecology Laboratory, Aiken, SC. SREL-38/UC-66e. 284 pp.
- COULTER, M.C. & A.L. BRYAN JR. (1988): Field Techniques and Methods of data collection used in studies of Wood Storks of the Birdsville colony and Swamps of the Savannah River Plant. Savannah River Ecology Laboratory, Aiken, SC. SREL. Univ. Georgia. 146 pp.
- DESAI, J.H., G.K. MENON & R.V. SHAH (1977): Studies on the reproductive pattern of the painted stork *Ibis leucocephalus* Pennant. *Pavo* 15 (1&2): 1-32.
- DRENT, R. (1975): Incubation. Pp. 333-420. In: Avian Biology, Vol. 5. (Eds: Farner, D.S. and J.R. King). Academic Press. New York.
- FARNELL, G. & P.W. SHANNON (1987): The breeding of Abdim's stork at the Audubon Park Zoo. *Colonial Waterbirds* 10(2): 251-254.
- FLEMING, R.L. SR., R.L. FLEMING JR. & L.S. BANGDEL (1979): Birds of Nepal, 2nd edn. Kathmandu. Avalok Publishers. Nepal. Pp. 358.
- HANCOCK, J.A., J.A. KUSHLAN & M.P. KAHL (1992): Storks, Ibises and Spoonbills of the World. Academic Press. New York. Pp. 391.
- HEINZMAN, G. & D. HEINZMAN (1965): Nesting of the Wood Stork. *Natural History* 74: 30-35.
- HUME, A.O. & F.W. OATES (1890): The nests and eggs of Indian birds. Second edition. Vol. 3. R.H. Porter. London. Pp. 461.
- KAHL, M.P. (1962): Bioenergetics of growth in nesting Wood Storks. *Condor* 62(3): 169-181.
- KAHL, M.P. (1964): The food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecological Monograph* 34: 97-117.
- KAHL, M.P. (1966): A contribution to the ecology and reproductive biology of the Greater Adjutant-Stork *Leptoptilos dubius* (Gmelin) and *L. javanicus* (Horsfield). *Ardea* 60: 97-111.
- KAHL, M.P. (1970): Observation on the breeding of Storks in India and Ceylon. *J. Bombay Nat. Hist. Soc.* 67: 453-461.
- KAHL, M.P. (1971): Social behaviour and taxonomic relationships of the storks. *The Living Bird* 10: 151-170.
- KAHL, M.P. (1972a): Comparative ethology of the Ciconiidae. Part 2. The adjutant storks *Leptoptilos dubius* (Gmelin) and *L. javanicus* (Horsfield). *Ardea* 60: 97-111.
- KAHL, M.P. (1972b): Comparative ethology of the Ciconiidae. The Wood Storks (Genera *Mycteria* and *Ibis*). *Ibis* 114: 15-29.
- KAHL, M.P. (1973): Comparative ethology of the Ciconiidae. Part 6. The Black-necked, Saddlebill and Jabiru Storks (Genera *Xenorhynchus*, *Ephippiorhynchus* and *Jabiru*). *Condor* 75: 17-27.
- KAHL, M.P. (1974): Comparative behaviour and ecology of Asian Storks. National Geographic Society Research Reports. Pp. 173-176.
- LACK, D. (1968): Ecological adaptations for breeding in birds. Methuen and Co. Ltd. London, 409 pp.
- MARKS, J.S. (1983): Prolonged incubation by a long-eared Owl. *J. Field Ornithol.* 54(2): 199-200.
- MEYERRIECKS, A.J. (1960): Comparative breeding

- behaviour of four species of North American Herons. *Nuttall Ornith. Club* 2: 1-158.
- MUNDKUR, T., P. CARR, SUN HEAN & CHHIM SOMEAN (1995): Survey for large waterbirds in Cambodia March-April 1994. Gland: IUCN.
- POMEROY, D.E. (1977a): Marabou Stork *Leptoptilos crumeniferus* breeding colonies in Uganda. *J. East Africa Nat. His. Soc. and National Museum*. 31(161): 1-11.
- POMEROY, D.E. (1977b): The biology of Marabou Storks in Uganda. I. Some characteristics of the species and the population structure. *Ardea* 65: 1-24.
- POMEROY, D.E. (1978a): The Biology of Marabou Storks in Uganda II. Breeding biology and general review. *Ardea* 66: 1-23.
- POMEROY, D.E. (1978b): Seasonality of Marabou Storks *Leptoptilos crumeniferus* in Eastern Africa. *Ibis* 120: 313-321.
- RAHMANI, A.R., G. NARAYAN & L. ROSALIND (1990): Status of the Greater Adjutant-Stork (*Leptoptilos dubius*) in the Indian Subcontinent. *Colonial Waterbirds* 13: 138-142.
- SAIKIA, P & P.C. BHATTACHARJEE (1989): A Preliminary Survey of adjutant storks in Assam. *Asian Wetlands News* 2(2): 14-15.
- SAIKIA, P & P.C. BHATTACHARJEE (1990): Nesting records of greater adjutant-storks in Assam, India. *Specialist group on Storks, Ibises and Spoonbills Newsletter* 3(1&2): 2-3.
- SAIKIA, P & P.C. BHATTACHARJEE (1996a): Studies on some aspects of the breeding biology of greater adjutant-stork, *Leptoptilos dubius* from the Brahmaputra Valley, Assam. *Tropical Zoology* 1(1): 57-64.
- SAIKIA, P & P.C. BHATTACHARJEE (1996b): Some aspects of the breeding biology of greater adjutant-stork *Leptoptilos dubius* in Brahmaputra Valley, Assam. In: Abstracts: Salim Ali Centenary Seminar on Conservation of Avifauna of Wetlands and Grasslands. Bombay Natural History Society, Mumbai.
- SCHUZ, E. (1972): Other stork species. In: Grzimek's Animal Life Encyclopedia, (Ed. Grzimek, H.C.). Van Nostrand Reinhold Co.
- SCOTT, J.A. (1975): Observations on the breeding of the Woolly-necked Stork. *Ostrich* 46(3&4): 201-207.
- SKUTCH, A.F. (1962): The constancy of incubation. *Wilson Bull.* 74: 115-152.
- THOMAS, B.T. (1984): Maguari Stork nesting: juvenile growth and behaviour. *Auk* 101: 812-823.
- THOMAS, B.T. (1985): Coexistence and behaviour difference among the three western hemisphere storks. Pp. 921-931. In: Neotropical Ornithology. (Eds: Buckley, P.A., M.S. Foster, E.S. Morton, R.S. Ridgely and F.G. Buckley) Ornithology Monogr. No. 36.
- THOMAS, B.T. (1986): The behaviour and breeding of adult Maguari Storks. *Condor* 88: 26-34.
- THOMPSON, A.L. (1950): Factors determining the breeding seasons of birds: an introductory review. *Ibis* 92: 173-184.
- TOMLINSON, D.N.S. (1976): Breeding behaviour of the great white egret. *Ostrich* 47: 161-178.
- URFI, A.J. (1993): Breeding pattern of painted storks (*Mycteria leucocephala* Pennant) at Delhi Zoo, India. *Colonial Waterbirds* 16(1): 95-97.

